V. *Notes on the Ancestry of the* Diptera, Hemiptera *and other Insects related to the* Neuroptera.*

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The greater part of winged insects now living may be grouped into two principal sections, one of which, the so-called Plecopteradelphia, or Plecopteron "brotherhood," contains the lower insects more closely related to the Plecoptera—such as the Blattoid superorder (Blattidae, Mantidae, Isoptera, Zoraptera, etc.), the Orthopteroid superorder (saltatorial Orthoptera, Phasmidae, Grylloblattidae, etc.), and the Plecopteroid superorder (Plecoptera, Embiidae, Dermaptera, Coleoptera, etc.), together with their fossil relatives; while the second section, the so-called Neuropteradelphia, or Neuropteron "brotherhood," contains the higher insects, more closely related to the Neuroptera—such as the Psocidæ, Mallophaga, Pediculidae, Hemiptera, Hymenoptera, Diptera, Mecoptera, Trichoptera, Lepidoptera, Neuroptera, etc., with their fossil relatives. In the following discussion the two sections described above may be referred to simply as the Plecopteron section (or group) and the Neuropteron section (or group).

It would be extremely difficult to find any features peculiar to all of the members of one section, and not occurring in any members of the other section; but it may be said of most of the insects belonging to the Plecopteron section, that their mouthparts are usually strongly mandibulate and well developed; while in the insects belonging to the Neuropteron section, the mouthparts of many are slender and greatly modified. In many of the insects of the Plecopteron group there is a marked tendency toward the reduction (and, in some cases, of a thickening) of the fore-wings; while in the insects of the Neuropteron

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section the fore-wings are frequently better developed than the hind ones. Long cerci (and in the males of some, styli also) are present in many of the insects belonging to the Plecopteron section; while in the insects belonging to the Neuropteron section they are wanting or vestigial as a rule, and in the latter insects the plates bearing the cerci ("paraprocts" or parapodial plates) are usually greatly modified or united with the terminal segments of the abdomen; while in the insects of the Plecopteron group they are usually distinct and well developed. Gonopod-like (*i. e.* forceps-like) genitalia are never found in the males of the Plecopteron section thus far examined, while this type of genitalia does occur in the males of some of the Neuropteron section. The type of metamorphosis (or lack thereof) exhibited by a group of insects is a matter of minor importance in the study of relationships, since in some families of insects such, for example, as the Coccidae, the males undergo a metamorphosis while the females of the same species do not. It may be stated, however, that with the exception of the Coleoptera, etc., the insects belonging to the Plecopteron section do not exhibit a marked metamorphosis; while many of the insects of the Neuropteron section (excepting the Psocidae, Hemiptera, etc.) exhibit a marked tendency in this direction.

So little is known of the anatomical details of the extinct fossil insects called Palaeodictyoptera (which have departed but little from the ancestral condition of winged insects in general) that it is impossible to determine their closest affinities. I believe, however, that the very ancient though somewhat aberrant orders Plectoptera (Ephemerida) and Odonata, among recent insects, are more closely related to certain Palaeodictyoptera than they are to either the Neuropteron section or the Plecopteron section, and I would therefore provisionally include the Plectoptera (Ephemerida) and the Odonata with the Palaeodictyoptera (and related fossil forms) in a third section of winged insects called the PLECTOPTERADELPHIA or Ephemerid "brotherhood," which will be referred to as the Ephemerid section, or group, in the following discussion.

In most (if not all) of the members of the Ephemerid section the wings cannot be folded along the abdomen (a very primitive condition), and the wing venation has departed but little from the original condition in many members of this group. Indications of a shifting of the

radial sector recently described in the Ephemerida (Morgan, 1912, Ann. Ent. Soc. Amer., 1912, p. 89) point to a rather close relationship to the Odonata, in whose wing venation a similar condition occurs, although it is unknown among other insects. In both Odonata and Ephemerida the antennae are usually much reduced, and they do not appear to be very large in most of the Palaeodictyoptera. The tarsi are composed of not over three segments in many of the insects of this section. Many of these insects have well-developed cerci (Bull. Brooklyn Ent. Soc., vol. 13, p. 49), although the cerci of certain Odonata have been otherwise interpreted by some investigators. In certain Ephemerid and Odonatan nymphs traces of a median unpaired terminal abdominal filament may be retained, and the abdominal segments are usually well developed in these insects. Paranota, or lateral expansions of the tergal region (Jour. N.Y. Ent. Soc., vol. 24, p. 1) occur on the abdominal segments, particularly those near the end of the abdomen, in certain immature Odonata and Ephemerida, and are occasionally retained on the last abdominal segments of the adult also. These and many of the characters mentioned above do not occur in all of the members of the Ephemerid section, nor are they characteristic of the members of this section alone, so that the only character peculiar to this group of insects and occurring in most of its members, is their inability to fold their wings flat along the abdomen.

Fig. 1.

Certain insects belonging to each of the sections mentioned above (*i. e.* the Ephemerid, Plecopteron, and Neuropteron sections) may occupy a position anatomically intermediate between the members of their own and of the other sections. The three sections may thus have a certain amount of "territory" in common, yet each taken separately forms a well-defined group in itself. If this were to be represented graphically, the three sections would be represented as three intersecting circles (Fig. 1) each of which taken separately forms a distinct well-defined division; yet in the area of overlapping they have a certain amount of territory in common. It would perhaps

have been more exact to represent these three groups as three intersecting spheres rather than as circles drawn in one plane; but the figure in question will serve well enough to illustrate the points under discussion.

The circle representing the Ephemerid group has been represented as though somewhat lower than that of the Plecopteron group, since certain Palaeodictyopteron members of the Ephemerid section are somewhat more primitive than the lowest representatives of the Plecopteron section. On the other hand, some members of the Ephemerid group may occupy a position extending up even into the territory of the Neuropteron group (as shown in the figure), since they have much in common with the lowest members of the Neuropteron section. As far as the more direct ancestors of the Neuropteron section are concerned, however, I would provisionally consider the Plecopteron section as more nearly representing their *immediate* ancestors, while the Ephemerid section may represent the common stock from which both the Plecopteron and Neuropteron sections are *ultimately* to be derived. On this account, the circle representing the Plecopteron group has been represented as though intermediate between the other two, in the figure.

Tillyard, 1917 (Biology of Dragonflies), emphasises the resemblance between the Protascalaphine Neuropteron *Stilbopteryx* and the Odonata, not only in appearance, but even in its mode of flight, etc., and it must be admitted that the Neuroptera are in many respects extremely like the Odonata and their allies, the Ephemerida. Handlirsch, 1906 (Die Fossilen Insekten), has also pointed out the marked resemblance of the Neuroptera to certain fossil Palaeodictyoptera, so that when one considers the Neuroptera alone, there is considerable evidence for regarding the Ephemerid section (*i. e.* the Ephemerida, Odonata, and Palaeodictyoptera) as more nearly representing the ancestral group giving rise to the insects related to the Neuroptera. The Psocidae, however, must be considered also in such a phylogenetic study, since they also occupy a position near the base of the lines of descent of the insects related to the Neuroptera, as is shown in Fig. 2; and a study of the affinities of the Psocidae is of no less importance than those of the Neuroptera, in attempting to determine the ancestry of the insects in question. Now the Psocidae exhibit undeniable affinities with the Coleoptera,

Dermaptera, Embiidae and Plecoptera, which constitute the Plecopteroid superorder (Jour. N.Y. Ent. Soc., vol. 25, 1917, p. 230), and, since the Neuroptera also exhibit many features in common with the Embiid and Plecopteron members of this same Plecopteroid superorder, I am inclined to consider that, taken as a whole (and not merely considering the Neuroptera alone), the lines of descent of the insects of the Neuropteron section would lead back to the Plecopteron section more directly, and ultimately

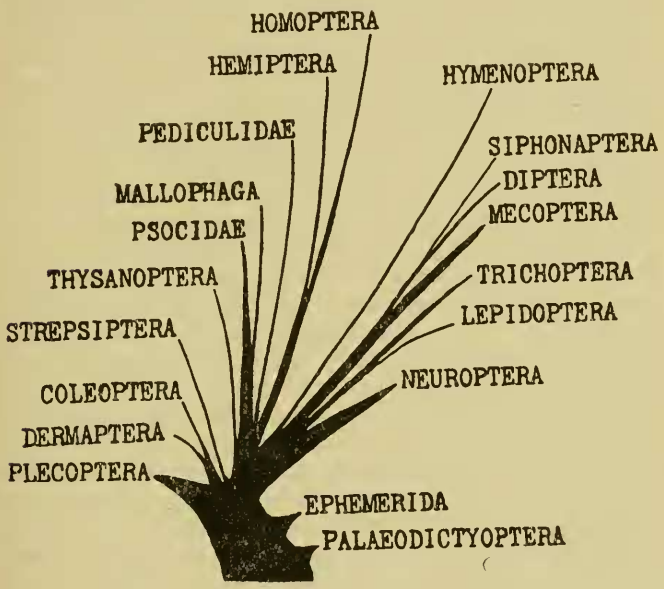

Fig. 2.

through or with them, to ancestors resembling the insects of the Ephemerid section. On this account, I have represented the Palaeodictyoptera and Ephemerida as occupying positions near the base of the common stem in Fig. 2, while the Plecoptera and their allies are shown somewhat nearer to the point where the lines of descent of the insects related to the Psocidae and Neuroptera have branched off.

It should be borne in mind that the diagram of the lines of descent shown in Fig. 2 is intended merely to aid in visualising the relative positions of the insects in question, and it does not accurately represent the actual inter-

relationships of these insects, since it would require a figure of three dimensions to show that one line of descent is in some cases intermediate between several others. Furthermore, it would make too complicated a figure to attempt to include in the diagram all of the lines of descent of the insects related to the ancestors of the Psocidae and the Neuroptera, so that but a few of these have been included in the diagram.

Among the most important of the insects omitted from the diagram shown in Fig. 2 are those comprising the Blattoid superorder (*i. e.* the Blattidae, Mantidae, Isoptera, Zoraptera and their fossil relatives), whose lines of development may be thought of as extending in a plane perpendicular to that containing the lines of descent of the Psocidae and Neuroptera. Now certain Mantidae, such as *Mantoida luteola*, are very Neuropteron-like, and certain Isoptera resemble the lower Psocidae, such as *Archipsocus*, very strongly, so that it is quite possible that the Blattoid superorder, to which these Mantids, Isoptera, etc., belong, more nearly represents the group ancestral to the Neuroptera than the Plecopteroid superorder does. Indeed, the Isoptera have even been classed with the "Neuroptera" by some entomologists who were apparently impressed with their Neuropteron-like appearance. On the other hand, the Embiid and Plecopteron representatives of the Plecopteroid superorder have likewise been classed as "Neuroptera" by some entomologists who were apparently impressed with the Neuropterous affinities of these insects, and when one takes into consideration the close relationship of the Psocidae to the Coleoptera, Dermaptera, Embiidae and Plecoptera (*i. e.* the Plecopteroid superorder) in addition to the marked resemblance of the Neuroptera to certain of these insects, there are very good reasons for considering the Plecopteroid superorder rather than the Blattoid superorder as more nearly representing the group which gave rise to the lines of descent of the insects related to the Psocidae and Neuroptera. In the foregoing discussion it should be clearly understood that the Plecopteron *section*, which includes the Blattoid, Orthopteroid and Plecopteroid superorders, is a more inclusive designation than the Plecopteroid *superorder*, which constitutes merely a portion of the insects included in the Plecopteron section.

It is perhaps a rather unfortunate choice to begin the discussion of the ancestry and interrelationships of the

insects related to the Neuroptera, with the consideration of such a highly aberrant and anomalous group as the Strepsiptera are, especially since their closest affinities are still a matter of considerable speculation. I feel, however, that the Strepsiptera occupy a position intermediate between the members of the Plecopteroid superorder, on the one hand (*i. e.* the Coleoptera, Dermaptera, etc.), and the insects grouped about the Neuroptera on the other. In order to bring out this fact, it was necessary to represent the Strepsipteron line of development in Fig. 2, as though branching off near the base of the Psocid-Neuropteron stem, although in reality the Strepsiptera are a strongly aberrant group structurally much higher than the Psocidae and Neuroptera. The line of development of the Strepsiptera should be thought of as though extending in a plane perpendicular to that of the lines of descent of the Psocidae and Neuroptera, since the Strepsiptera appear to occupy a position intermediate between the Coleoptera, on the one hand, and the insects related to the Neuroptera and Psocidae on the other. Pierce, 1909 (Smithsonian Bull. 66), is inclined to regard them as more nearly related to the Dipteron group of the insects allied to the Neuroptera, and Latreille, 1809 (Genera Crust. et Insect., vol. 4), at first placed them with the Diptera also. Haeckel, 1896, would group them with the Neuropterous insects. Rossi, 1793 (Bull. Soc. Philom., vol. 1), thought that they were related to *Ichneumon* among the Hymenoptera, while Gegenbauer, 1859 (Grundz. vergl. Anat., first edition), considers that their closest affinities are with the Trichoptera (as does Gerstaecker), and Shuckard, 1840, places them between the Forficulidae and Phryganidae. Most investigators, however, agree in placing them among or next to the Coleoptera. In previous papers I have called attention to certain resemblances between the Strepsiptera and the Psocidae with the Hemipteroid insects, and I still believe that there are many points of resemblance between the Strepsiptera and the insects related to the Psocidae and Hemiptera (*sensu lato*), so that, provisionally at least, we may regard the Strepsiptera as occupying a position intermediate between the Coleoptera, etc., on the one hand, and the Psocidae and Hemiptera on the other, although the Strepsiptera likewise exhibit some marked affinities with the Neuropteroid insects as well.

The Thysanoptera are another strongly aberrant order

related to the Psocidae, and to the Hemiptera (with the Homoptera). They have likewise carried over in their line of development some of the characters occurring in certain representatives of the saltatorial Orthoptera, and in the Forficulid representatives of the Plecopteroid superorder. We thus have another threefold resemblance which makes it rather difficult to determine the closest affinities of the insects in question; but the generally accepted opinion that the Thysanoptera are rather closely related to the Hemiptera (*sensu lato*) appears to be well founded. Boerner, 1904 (Zool. Anzeiger, Bd. 28, p. 511), has pointed out the resemblance of the parts of the head of Thysanoptera to those of Psocidae and Hemiptera (*sensu lato*), and the evidence furnished by a study of the head region is borne out by that of other parts of the body as well. On the other hand, Hood, 1915 (Proc. Biol. Soc. Washington, 28, p. 53), regards the Thysanoptera as "Orthopteroid" insects, following Handlirsch, 1909 (Die fossilen Insekten), who derives both Thysanoptera and Dermaptera from forms related to the saltatorial Orthoptera such as the "Locustids" and Gryllids. According to Hinds, 1902 (Proc. U.S. Nat. Museum, vol. 26, p. 79), "about 1828, through the anatomical studies of Straus-Duerckheim and Latreille, sufficient evidence was obtained to lead Latreille to separate the Thysanoptera from the Hemiptera and place them among the Orthoptera," and Jordan, 1888 (Zeit. Wiss. Zool., Bd. xlvii, p. 541), thought that the Thysanoptera should be classed "according to their immersed germ band and their larval form in the line of the Orthoptera, Homoptera, Hemiptera, wherein they should be placed according to their anatomy and biology." Jordan also states that "if we collect the Mallophaga, Psocidae and Termitidae as Corrodentia with Brauer, then we must place Thysanoptera in the system between Corrodentia and Hemiptera" (*teste* Hinds, 1902), and in this respect his views are not essentially different from those here given. According to Jordan, some of his predecessors have regarded the Thysanoptera as related to the Odonata, but there does not seem to be much evidence to support this view.

As was mentioned above, the Strepsiptera and Thysanoptera are highly aberrant insects whose closest affinities are extremely difficult to determine. On the other hand, the Psocidae, together with the Neuroptera, furnish us

with the intermediate links connecting the higher insects, such as the Hemiptera, Diptera, etc., with the lower forms, and the study of such primitive Psocidae as *Archipsocus*, for example, is of the utmost importance in attempting to determine the ancestry of the higher insects here discussed. Brauer, as was stated in the preceding paragraph, groups the Mallophaga, Psocidae and Isoptera together as Corrodentia, and Enderlein, 1903 (Zool. Anzeiger, 26, p. 423; see also Palaeontographia, 1911, Bd. 58, p. 279), apparently influenced by Brauer, groups the Psocidae, Mallophaga, Isoptera and Embiidae in the single order Corrodentia, to which Escherich, 1914 (Handw. buch d. Naturw.), would add the Pediculidae also. All of the foregoing investigators agree in regarding the Isoptera as quite like the ancestors of the Psocidae; and Handlirsch, 1909 (*l.c.*), would derive the Psocidae, together with the Isoptera, from Blattoid ancestors (as does Mjoberg), thus agreeing with them in substance. On the other hand, Kolbe, 1901 (Arch. f. Naturg. lxvii, Beigeft, p. 89), was apparently impressed with the marked affinities between the Psocidae and the Dermaptera (Forficulids) with the Coleoptera, although he is mistaken in believing that the Dermaptera and Coleoptera could be derived from ancestors like the Psocidae, since the Dermaptera are much more primitive than the Psocidae are.

In a measure, all of the views cited above are correct, since the Psocidae were doubtless descended from ancestors resembling the Plecopteroid superorder and would therefore naturally have certain features in common with the Plecopterous, Embiid, Forficulid, and Coleopterous representatives of this superorder. Similarly, since the Isoptera were also very probably descended from ancestors resembling the same Plecopterous superorder, it is not surprising that both Psocidae and Isoptera should have certain points in common with each other and with certain members of the ancestral Plecopteroid superorder, having taken over in their lines of descent certain similar features from their common heritage. On the other hand, when we take all of the anatomical details into consideration, the closest affinities of the Isoptera are seen to be with the Blattoid superorder (Blattidae, Mantidae, Isoptera and Zoraptera), and the closest affinities of the Embiidae are with the Plecopteroid superorder (Plecoptera, Embiidae, Forficulidae, and Coleoptera), while the closest affinities

of the Psocidae appear to be with the insects grouped about the Neuroptera, with which they are connected by intermediate forms. The Isoptera, Embiidae and Psocidae cannot therefore be grouped together, since they belong to three divergent lines of descent; but, since these divergent lines of descent had a common origin, the lowest representatives of each would naturally have preserved many features in common with the other two. In deriving the Psocidae from ancestors related to the Embiidae and other members of the Plecopteroid superorder, I would not minimise the very evident affinities between the Psocidae and Isoptera, since subsequent investigation may prove that the ancestors of the Psocidae are much closer to the Isoptera than they are to the Embiidae, Dermaptera, etc. Provisionally, however, I would regard their ancestors as somewhat more closely allied to the Embiidae, Dermaptera, Coleoptera, and the other members of the Plecopteroid superorder.

As was mentioned above, Brauer emphasised the relationship of the Mallophaga to the Psocidae, and placed them both in the order Corrodentia; but he was doubtless incorrect in including the Isoptera in this order also. Packard, 1887 (Amer. Phil. Soc. 1887, p. 264), places the Mallophaga in the order "Platyptera," which includes the Plecoptera and Embiidae in addition to the other insects mentioned above; but this grouping contains too many discordant elements. Kellogg, 1902 (Psyche, vol. 9, p. 339), and others have emphasised the remarkable resemblance between the Mallophaga and the Psocidae, and there can be but little doubt that the Mallophaga are very closely related to the Psocidae and to the Pediculidae as well, so that there can be no serious objection to the view that the Mallophaga arose from ancestors very like the Psocidae as shown in the diagram of the lines of descent of these insects.

The Pediculidae (also called Suctoria, Anopleura, or Siphunculata) are undoubtedly closely related to the Mallophaga, as has been pointed out by Cummings, 1910 (Ann. Mag. Nat. Hist., vol. 15, p. 256), Mjoberg, 1910 (Arkiv f. Zoologi), and many others, following Leach, 1817. Enderlein, 1904 (Zool. Anz., vol. 28, p. 121), emphasises the relationship of the Pediculidae to both the Mallophaga on the one side and the Hemiptera on the other, and indeed, most of the earlier writers placed the

Pediculidae with the Hemiptera (*sensu lato*). Since the Pediculidae have many points in common with both Mallophaga and Hemiptera (with the Homoptera), their line of descent has been represented in the diagram as though intermediate between that of the Mallophaga (with the Psocidae) and the Hemiptera (with the Homoptera).

The Hemiptera and Homoptera are extremely closely related, and are usually grouped in a single order; but there are very good grounds for considering that the insects so classed should be divided into at least two orders—the Hemiptera (*sensu stricto*) and the Homoptera —although the further division of the Homoptera into other orders by Handlirsch, 1909 (Die Fossilen Insekten), is doubtless too extreme.

In discussing a paper by Osborn, 1894 (Proc. Ent. Soc., Washington, vol. 3, p. 190), on the phylogeny of the Hemiptera, Ashmead suggests that the "Pediculidae are the oldest forms representing the stem from which sprang the Homoptera in one direction and the Heteroptera in another." Most of those who group the Pediculidae with the Hemiptera, however, regard them as "degenerate" Hemipteroid insects. Paul Meyer, 1876, who derives the Hemiptera (with the Homoptera), together with the Pediculidae and Mallophaga, from a "Protohemipteron" stem apparently paved the way for the modern view of the interrelationships of the Hemiptera, Pediculidae, Mallophaga, etc., expressed by Enderlein, 1904 (Zool. Anz., Bd. 28, p. 121), and particularly by Boerner, 1904 (Zool. Anz., Bd. 27, p. 511), who groups the Psocidae, Mallophaga, Pediculidae, Thysanoptera and Hemiptera (with the Homoptera) in a section which he calls the "Acercaria." Handlirsch, 1909 (*l.c.*), however, following certain earlier investigators, is more impressed with the Neuropteroid affinities of the Hemiptera (and Homoptera) as exhibited by such fossil forms as *Eugereon boeckingi* described by Dohrn, 1867 (Stett. Ent. Zeit., Bd. 28, p. 145), although Kirkaldy, 1910 (Proc. Hawaiian Ent. Soc., vol. ii, p. 117), thinks that *Eugereon* is not "even a Hemipteroid insect" but is "a Neuropteroid insect of a kind that has no representatives in modern times, that has become extinct, forming an order or suborder of its own." In several papers I have called attention to the Neuropteroid character of the thorax of such lower

Homoptera as *Cicada* (see also Taylor, 1918, Ann. Ent. Soc. America, vol. 11, p. 225), and if *Eugereon* is really a Hemipteroid insect, it would certainly point to a very close relationship between the ancient Hemiptera and the Neuroptera. Furthermore, the nature of the mouth-parts (*e. g.* union of labial palpi, etc.), head, and other structures in the Hemiptera, are quite suggestive of the condition occurring in insects descended from Neuroptera-like forbears—such as the Mecoptera and their relatives the Diptera, and there are evidences of a relationship to the lower Lepidoptera also (which are members of this group), so that there are very good grounds for considering that the Hemiptera are related to the Mecoptera and other insects descended from Neuroptera-like forbears. McLeay, 1821–1825, apparently realised the affinities between the Hemiptera and certain of the members of the Neuropteroid superorder, for, according to Handlirsch, in articles published in vol. 2 of the Horae Ent., and vol. 14 of the Linn. Trans., McLeay groups the Homoptera, Hemiptera, Siphonaptera, Diptera and Lepidoptera together as "Haustellata"—a grouping adopted by Agassiz, 1851 (Classif. of Insects from Embryol. Data), and in part by Haeckel, 1866 (Generelle Morphologie), who places the Hemiptera, Homoptera, Pediculidae, Diptera and Lepidoptera in his subclass "Sugentia." Kolbe, 1884 (Berl. Ent. Zeit., Bd. 28, p. 169), regards the Hemiptera as a "neotypic offshoot" of the "Orthoptera," while, as far back as 1831, Latreille, in his Cours d'Entomologie, classes the Coleoptera, Dermaptera, Orthoptera and Hemiptera in the group called Elythroptera (or Elytroptera of Dana, 1864), on the basis of the thickening of the fore-wings. Schoch (Schw. Ent., Bd. 7) derives the Hemiptera from forms related to the Odonata.

There are many other groupings of the Hemiptera, but the ones which appear to be the most in accord with the facts of comparative anatomy are those which place the Hemiptera with the insects grouped about the Neuroptera or the Psocidae. While the Hemiptera (with the Homoptera) exhibit undeniable affinities with the Neuroptera and their allies, it is likewise quite evident that the Hemiptera are no less closely related to the Psocidae and their allies, and provisionally, at least, I would regard them as somewhat more closely related to the Psocidae and their allies than to the members of the Neuropteroid super-

order. The lines of descent of the Hemiptera and Homoptera have therefore been represented in the diagram as though occupying a position intermediate between the insects grouped about the Neuroptera and those grouped about the Psocidae, being slightly nearer the latter than the former.

The Hymenoptera are here treated as though constituting a single order; but there are some grounds for considering the sawfly group, or chalastogastrous Hymenoptera (including the suborder Idiogastra of Rohwer, 1917, Proc. Ent. Soc. Washington, vol. 19, p. 92) as a distinct order, called Prohymenoptera by Crampton, 1916 (Ent. News, vol. 27, p. 303), or Bomboptera by MacLeay, 1829 (applied to the "Uroceridae" alone). Rohwer, 1917 (*l.c.*), however, points out the annectant character of the Oryssoid sawflies between the Siricoid members of the sawflies and the Braconids, etc., among the higher Hymenoptera, maintaining that this connection between the two groups unites them into one homogeneous order. When one has examined such "synthetic" types as the Micropterygidae, Zoraptera, Grylloblattids, Isoptera, etc., which combine in themselves characters common to several other orders of insects, it is at once apparent that the existence of these connecting forms does not invalidate the distinct orders which they serve to connect (and indeed, at one time, all of the orders must have been connected by such intermediate forms), so that Rohwer's objection to the division of the Hymenoptera on this score, does not hold good. For the sake of convenience, however, they are treated as a single order in the present discussion.

Ashmead, 1895 (Proc. Ent. Soc., Washington, vol. 3, p. 330), has summarised the different views as to the relationships of the Hymenoptera, as follows: "Latreille placed it (the order Hymenoptera) between the Neuroptera and the Lepidoptera, regarding *Phryganea* and *Termes* as forming the link between them, considering the long-tongue bees as approaching nearest to the Lepidoptera. MacLeay, on the other hand, placed the Hymenoptera between the Coleoptera (with which they are supposed to be connected by the osculant order Strepsiptera) and the Trichoptera, the Tenthredinidae being considered as Trichopterous and the Uroceridae as forming an osculant order Bomboptera, between Trichoptera and Hymenoptera, which last order is reduced to the species possessing apodal

larvae. . . . Packard, 1863 (Boston Jour. Nat. Hist., 7, p. 591), in his paper entitled 'On Synthetic Types in Insects,' says that the Coleoptera, Hemiptera, Orthoptera and Neuroptera seem bound together by affinities such as those that unite by themselves the bees, moths and flies, and to the latter, or what he considers the higher series, he has since applied the term Metabola, and to the former Heterometabola. . . . Packard also believes the Hymenoptera are descendant from the Lepidoptera." In his diagram of the lines of descent of the orders of insects, Ashmead (*l.c.*) derives both Lepidoptera and Hymenoptera from a Trichopteroid stem. Schoch, 1884 (Schw. Ent., Bd. 7), derives the Hymenoptera, Lepidoptera, and Diptera from Neuroptera. Paul Meyer, 1876, thinks that the Hymenoptera are closely related to the Orthoptera. Sajo, 1908 (Prometheus, Bd. 19, p. 705), thinks that the Hymenoptera are very closely allied to the Coleoptera, and Handlirsch (Fossilen Insekten) is apparently of the same opinion, since he derives both Hymenoptera and Coleoptera from forms related to the Protoblattoidea, suggesting that the Mantidae are intermediate between the Protoblattoidea and the Hymenoptera. In previous papers I have pointed out the resemblance between certain adult sawflies and the Mecoptera such as *Panorpodes*, *Merope*, etc., and a further study has convinced me that the sawflies are quite closely related to the Mecoptera, as well as to the Psocidae, occupying a position intermediate between the two groups, but being a little more closely related to the Mecoptera than to the members of the other group. I find that others have also noted the resemblance between the Hymenoptera and Mecoptera, for Ashmead, 1895 (Proc. Ent. Soc. Wash., 3, p. 331), states that "the larvae of the Mecoptera also approach close to the Hymenoptera, and the peculiar rostrate head of the imagoes of this order is frequently reproduced among the parasitic species *Agathis*, *Cremnops*, etc.," and Kolbe, 1884 (Berl. Ent. Zeit., 28, p. 169), calls attention to the presence in both Hymenoptera and Panorpidae of "primitive biting mouthparts, similar wing venation, and similar formation of the thoracic segments" in the adults, and the similar caterpillar-like larvae present in both orders. The larvae of sawflies which I have examined (Crampton, 1918, Proc. Ent. Soc., Washington, 20, p. 59) "resemble those of the Panorpids in having retained the

lateral cervical plates"; but in certain other respects, the sawfly larvae are more similar to Lepidopterous larvae.

The venation of the wings of certain sawflies, particularly in the anal region, is strongly suggestive of the condition occurring in the wings of some of the more primitive Psocidae, and I find indications of a relationship between the two in certain features of the head and thorax (especially the tergal region). On the other hand, the nature of the male genitalia of the sawflies is surprisingly like the genitalia of male Mecoptera, the shape of the head and the nature of the mouthparts, etc., are much more similar in the sawflies and Mecoptera, and on the whole the closest affinities of the Hymenoptera appear to be with the Mecoptera and other insects grouped about the Neuroptera. I have therefore represented the Hymenoptera in the diagram as a very primitive group occupying a position somewhat intermediate between the insects grouped about the Psocidae and those grouped about the Neuroptera, with their strongest affinities on the side of the Neuropteroid forms such as the Mecoptera. The similarity between the wing veins of the Diptera and sawflies pointed out by MacGillivray, 1906 (Proc. U.S. Nat. Museum, 29), and others would thus be readily explained by the fact that Diptera are descended from Mecoptera-like forbears, and if the sawflies resemble Mecoptera, they would naturally be similar in some respects to the Diptera also. In the same way, the resemblances between the Hymenoptera and the Trichoptera or Lepidoptera might be explained as the result of their mutual relationship to the Mecoptera. In some respects the Hymenoptera are quite like the Neuroptera, and the latter group may possibly represent the ancestral forms from which the Hymenoptera were derived; but it is more probable that the ancestors of the Hymenoptera were very primitive forms occupying a position intermediate between the Neuroptera and the Psocidae.

Most modern investigators agree in regarding the Siphonaptera, Suctoria, or Aphaniptera as the descendants of forms very like the Diptera; and their ancestors were probably quite similar to the Dipteron family Phoridae. The Siphonaptera have therefore been represented in the diagram as a lateral branch of the main Dipteron line of development, although as Packard, 1895 (Proc. Boston Soc. Nat. Hist., 26, p. 354), states, "they must have

diverged from the ancestral Dipterous stem before the existing forms of Diptera had become so extremely specialised as we now find them to be." According to Packard (*l.c.*) Haliday considered the fleas as "a group of Diptera allied to the Mycetophilidae"; . . . "those who regarded them (the fleas) as Diptera were Roesel, Oken, Straus-Duerckheim, Burmeister, Haliday, Newman, Walker, von Siebold, with many German entomologists, and J. Wagner (1889). They were regarded as Hemiptera by Fabricius and by Illiger. . . . The fleas were placed by MacLeay and by Balbiani between the Diptera and Hemiptera; by Leach between the Hemiptera and Lepidoptera; by Dugès between the Hymenoptera and Diptera; and by Brauer they are given a position between the Diptera and Coleoptera." Brues, 1901 (American Naturalist, 35, p. 336), discusses the relationship of fleas to Phoridae, and Dahl, 1897 (Zool. Anz., 20, p. 409), describes a Phorid, *Pulicophora*, which he considers annectant between the Phorids and fleas, although Wandolleck, 1898 (Zool. Anz. and Wiss. Rundschau), takes exception to Dahl's statements on the subject.

The Diptera are undoubtedly as closely related to the Mecoptera as to any other order of insects, and the Mecoptera have apparently departed as little as any living forms from the type ancestral to the Diptera, so that the Dipteron line of development has been represented in the diagram as though merging with that of the Mecoptera, as we trace them both back to their common Neuroptera-like ancestors. As was mentioned in previous papers, I find in such Neuroptera as *Nemoptera*, many features suggesting the presence of tendencies in the Neuropteron stem which are later to find opportunity for fuller expression in the development of the Dipteron type of insects. Among these may be mentioned the tendency toward the formation of the elongate type of head in *Nemoptera*, the reduction of the hind-wings in this insect (which if carried a little further would result in the production of a halter-like structure), and the character of the genitalia in males of *Nemoptera*. On the other hand, the resemblance between the lower Diptera such as the Tipuloid forms and the *Bittacus*-like representatives of the Mecoptera is very striking and extends even to the more minute details, the head and mouthparts, thoracic sclerites, and genitalia being very similar in the two groups—and

I have even found a genital structure in the males of the Tipulid *Pachyrhina macrophallus* described by Dietz, 1918 (Trans. Amer. Ent. Soc., 44, p. 105), strongly suggestive of the coiled spring-like structure in the genitalia of males of *Bittacus*. The resemblance between the genitalia of the males of both groups has been pointed out in a paper published in Psyche, 1918, vol. 25, p. 55, and the evolution of the head types in Neuroptera, Mecoptera and Diptera has been traced in a paper published in the Annals Ent. Soc. America; 1918, vol. 10, p. 337. As was pointed out in the paper on the evolution of the head types in Diptera, etc., the Trichoptera have retained certain features suggestive of the ancestors of the Diptera (and Packard, 1883, derives the Diptera from them); but this may possibly be explained as the result of the relationship of both Diptera and Trichoptera to the Mecoptera, since the Diptera and Trichoptera were in all probability descended from ancestors not unlike the Mecoptera (or from the Neuroptera-like ancestors of the Mecoptera). Similarly, since the Lepidoptera were descended from ancestors resembling those of the Trichoptera and Mecoptera, they therefore might also carry over certain characters in common with the Diptera, which are derived from a similar ancestry. I would thus account for the resemblances of the Lepidoptera, Trichoptera, Hymenoptera, etc., to the Diptera, as the result of their common or mutual relationship to the Mecoptera (or the Neuropteroid ancestors of the Mecoptera). If it should prove to be the case that the Homoptera (and Hemiptera) are more closely related to the Mecoptera and other Neuropteroid insects than to the Psocidae and their allies, the slight resemblance of the Hemiptera to the Diptera might in the same way be explained as the result of their mutual relationship to the Mecoptera. At present, however, I do not think that the Homoptera are very closely related to the Diptera, while the Lepidoptera do show some unmistakable resemblances to the Diptera, as is also the case with the Trichoptera, and to some extent, the Hymenoptera also.

Whether the ancestors of the Diptera would have been placed in the order Mecoptera by systematists, or whether they were Neuroptera-like forms giving rise to both the Dipteron and Mecopteron lines of descent, I cannot say; but it is quite evident that the Mecopteron line of descent has paralleled that of the Diptera more closely and for a

further distance than has that of any other order, and the Mecoptera have apparently departed but little from the ancestral condition of the Diptera. Handlirsch derives both Diptera and Lepidoptera from a common Mecopteron stock, and also derives the Trichoptera from the same stem which he traces back to the fossil Megasecoptera. Many of the older entomologists grouped the Diptera with the Strepsiptera on account of the presence in both of only two wings, although the wings are borne on different segments of the thorax in the two groups of insects. Dana, 1864, places the Hymenoptera, Diptera and Siphonaptera in his division "Apipiens" (of his "Ctenoptera") corresponding to the "Metabola" of Packard 1863–1870, who in 1883 added the Lepidoptera to the group and called them all "Euglossata"; while Schoch, 1884, calls the Diptera, Lepidoptera and Hymenoptera, "Zygothoraca." Haeckel, 1866, groups the Hemiptera (*sensu lato*), Pediculidae, Lepidoptera, and Diptera together as "Sugentia," and derives the Diptera from Hemiptera, while Ashmead, 1895, derives the Diptera in part from the Hemiptera (Homoptera) and partly from the Mecoptera. Smith, 1897 (Science, N.S. 2, vol. 5, p. 671), groups the Hymenoptera, Siphonaptera, Diptera, Mecoptera, Lepidoptera, Trichoptera, Odonata and Ephemeridae together—a grouping which is quite like that here accepted if the Odonata and Ephemeridae were omitted, and the Neuroptera substituted in their place. Boerner, 1904 (Zool. Anz., 27, p. 532), groups together the Mecoptera, Diptera, Siphonaptera and Hymenoptera in the section "Cercophora" of the Holometabola, and with the exception of his including the Coleoptera among the insects related to the Neuroptera, his derivation of the lines of descent of the insects in question is essentially similar to that here given. Formerly I suggested that the Nycteribiid Diptera have departed widely from the other Diptera, and that their Braulid relatives have departed sufficiently far to be classed in a distinct order (Ent. News, 27, p. 302); but this view is too extreme, for the pupiparous Diptera are connected with the remainder of the order by intermediate forms, and should be included with them in the homogeneous order Diptera, since the winged forms are evidently Diptera. It is rather interesting to note in this connection, that one hundred years ago Leach, 1817 (Zool. Misc., vol. 3), had proposed to place the Pupipara in a separate order

called Omaloptera (or the Homaloptera of Westwood, 1839).

The grouping of the Mecoptera with the Neuroptera by the earlier entomologists was apparently well founded, since the Neuroptera certainly seem to represent as nearly as any living forms, the ancestral type from which the Mecoptera were derived. The group Planipennia contains the types approaching as closely as any Neuroptera to the ancestral Mecoptera, and such Neuroptera as *Nymphes* (and in some respects the Ithoniidae also) have retained certain features very suggestive of Mecopteron affinities, although I have always felt that the Nemopteridae are very like some of the ancestors of the Mecoptera—especially those in which the head had begun to take on the elongate form. Handlirsch (*l.c.*) derives the Mecoptera from the fossil Megasecoptera. Lameere, 1908 (Ann. Soc. Ent. Belgique, 52, p. 139), agrees with Handlirsch in this derivation of the Mecoptera, and there is much to be said in favour of this view. Lameere would derive the Neuroptera as well as the Mecoptera (and their allies) from the Megasecoptera, instead of deriving the Neuroptera from the Palaeodictyoptera as Handlirsch does (although the Megasecoptera are themselves derived from Palaedictyopterous forbears), and Lameere's view would more nearly harmonise with the evident relationship of the Mecoptera to the Neuroptera, both groups being evidently descended from common ancestors, from which the Neuroptera have departed much less than the Mecoptera have. Since the fossil forms (with the exception of the Palaeodictyoptera) are not represented in the diagram, the line of development of the Mecoptera has been drawn as though extending back to the common Neuropteron stem. The Mecoptera form an extremely important group from the standpoint of phylogeny, since their line of descent is paralleled by, or is approached by those of so many other Neuropteroid insects, and it is to be hoped that the researches of Dr. Tillyard,* who has an extensive knowledge of the insects in question and who also has access to the most primitive

* Since writing the above, I have received from Dr. Tillyard a separate of a paper on the "Panorpoid Complex" (Proc. Linn. Soc. N.S.W., xliii, 1918, p. 265) in which he states that "the origin of the Panorpoidea from the Megasecoptera is not supported by a single piece of evidence worth considering," although he does not attempt to determine the ultimate ancestry of the Mecoptera.

representatives of the Mecoptera and their allies, will soon definitely determine the ultimate affinities of these insects.

The Trichoptera are extremely closely related to the Neuroptera, and were classed with them by the earlier entomologists. On the other hand, the Trichoptera are quite closely related to the Mecoptera also, and are derived from the Mecopteron stem by Handlirsch 1909 (*l.c.*) who, strange to say, represents the Dipteron line of descent as though branching off from the same stem at a lower point, whereas the Trichoptera are morphologically more primitive than the Diptera and have retained certain features which were probably present in the ancestors of the Diptera. Packard, 1883 (Third Rpt. U.S. Ent. Commission, p. 295), who derives the Diptera from the Trichoptera, groups the Mecoptera, Trichoptera and Neuroptera together in his order "Neuroptera," and traces the Trichopteron line of development to a Mecopteron stem, thus agreeing with Handlirsch's derivation of the Trichoptera. On the basis of the character of the ovaries, Emery groups the Trichoptera with the Coleoptera Adephaga, Neuroptera, Mecoptera, Lepidoptera, Diptera and Hymenoptera as "Metabola ovariis meroisticis" (*teste* Handlirsch), thus essentially agreeing with the view here expressed, save that the Coleoptera are not included with these insects. Sharp, 1889, according to Handlirsch, designates the insects called "Metabola ovariis meroisticis" by Emery, as the "Endopterygota," on the basis of the internal formation of the wings. Boerner, 1904 (*l.c.*), groups the Trichoptera, Lepidoptera, Neuroptera, Coleoptera and Strepsiptera together as the section "Proctanura" of his Holometabola. Leach, 1817, with his usual keenness of insight links together the Trichoptera and Lepidoptera in a group to which Haeckel, 1896, applies the term "Sorbentia" (one of his six "legions"). As was mentioned above, the Trichoptera are very closely related to the Neuroptera on the one hand, and to the Mecoptera on the other, and were probably descended from the Neuroptera-like ancestors which gave rise to the Mecoptera. They are undoubtedly very closely related to the Lepidoptera; but do not seem to have much in common with the Homoptera, with which Dana, 1864, groups them in his division "Amplipens" of the group "Ctenoptera."

The Lepidoptera are related to the Trichoptera, Neuroptera and Mecoptera; but their strongest affinities are

apparently with the Trichoptera, as Leach, 1817, pointed out a hundred years ago. Speyer, 1839 (Oken's Isis, 1839, p. 94), suggested that the Micropterygids form a transitional group leading to the Trichoptera, and later in 1870 (Stettin. Ent. Zeitung, 1870, p. 202) he carried the comparison between the two groups still further. Chapman, 1893 (Trans. Ent. Soc. London, 1893, p. 255), calls attention to the huge mandibles of the pupa of *Micropteryx purpurella* (originally figured by Stainton in the Entomologist's Annual) which certainly resemble those of certain Trichopterous pupae, and on p. 569 of the Trans. Ent. Soc. London, 1896, Chapman * says, "I believe Dr. Sharp quite agrees with me in assimilating the Phryganeidae and Micropterygidae together as being, though somewhat far apart, still nearer together than either is to the Neuroptera on the one hand, or to the Lepidoptera on the other. I believe he sets more value on their Neuropterous than on their Lepidopterous affinities, whilst I take rather the contrary view, regarding the lower Adelidae as being very probably directly derived from the Micropteryges." Comstock, 1918 (The Wings of Insects, pp. 307, 313, 317), is so deeply impressed with the Trichopterous affinities of the Micropterygidae, that he removes them from the Lepidoptera and places them in the Trichoptera as a suborder of the latter group; but the Lepidopterous structures present on the Micropterygidae clearly indicate that they belong in the order Lepidoptera. Koletani, 1858 (Wien Ent. Monatschr., 2, p. 381), considers that the "aquatic" Lepidopteron *Acentropus niveus* is annectant between the Trichoptera and Lepidoptera, and since such Trichoptera as *Plectrotarsus gravenhorsti* have actually developed a *coiled proboscis* (!) like that of certain Lepidoptera one can hardly ignore the close relationship between the Lepidoptera and Trichoptera. Since the Trichoptera have remained more primitive than the Lepidoptera, although accompanying the latter insects for a considerable distance along the same developmental road, they may be considered as near as any living forms to the ancestors of the Lepidoptera. While emphasising the similarity between the wings of Lepidoptera and Trichoptera, Kellogg, 1895 (Amer. Naturalist, 29, p. 718), calls

* Dr. Tillyard informs me that Chapman places the *Micropteryx*-like forms in an order distinct from the Lepidoptera, called the Zeugloptera, in a later publication; but I have been unable to locate the reference.

attention to the resemblance of the wings of the Mecoptera to those of Lepidoptera, and Tillyard, 1918 (Ent. News, 29, p. 90), states that " the result of the study of five genera of the family Micropterygidae (*s.l.*, including the Eriocraniidae) is that I find them all to be, not of the jugate type of the Hepialidae, but of a more primitive jugofrenate type, in which the wing-coupling apparatus closely resembles that of the Planipennia, Megaloptera and Mecoptera." Tillyard has also called attention to the resemblance between certain Australian Hepialid Lepidoptera and the Ithoniid Neuroptera.

As was the case with the Diptera in which it is extremely difficult to determine whether their line of development branched off from that of the Mecoptera (to which they are so closely related) or whether it extends parallel to that of the Mecoptera back to the Neuroptera-like ancestors giving rise to both Mecoptera and Diptera, so with the Lepidoptera, it is extremely difficult to determine whether their line of development branches off from that of the Trichoptera (to which they are extremely closely related), or extends parallel with the Trichopteron line of development back to the Neuroptera-like ancestors of both Lepidoptera and Trichoptera. This much, however, is true, that the Neuroptera have departed the least of any living insects from the ancestral condition of those forms giving rise to the lines of development of the Mecoptera, Trichoptera, Lepidoptera, etc. Packard, 1883 (*l.c.*), would derive the Lepidoptera from the Diptera, which in turn are derived from Trichoptera and these from Mecoptera, thus ultimately deriving them all from a common stock not unlike the Mecoptera. In this respect, his views are somewhat like those of Handlirsch (*l.c.*), who derives the Trichoptera, Lepidoptera, Diptera, etc., from the Mecopteron stem, which he traces back to Megasecopterous ancestors. Lameere, 1908 (Ann. Soc. Ent. Belgique, 52, p. 139), says, " I am completely in accord with Handlirsch with regard to the composition of this systematic unity (Handlirsch's group ' Panorpoidea ') comprising the Mecoptera, Trichoptera, Lepidoptera, Siphonaptera and Diptera " (Lameere, however, uses other terms for these orders), and " I consider with Handlirsch, that this first group of the Holometabola is descended from the Megasecoptera." It is difficult to understand, however, why neither Handlirsch nor Lameere include the Neuroptera also among the

" Panorpoid " insects, especially since Lameere would derive the Neuroptera from the same Megasecopterous stem with the " Panorpoid " insects.

Handlirsch, 1909 (*l.c.*), suggests that the order Neuroptera should be divided into at least three orders, the Megaloptera (Sialidae and Chauliodidae), the " Raphidoidea," and the true Neuroptera. Of these he makes a subclass " Neuropteroidea " of equal value with his subclass Orthopteroidea containing such widely divergent forms as the Acridiidae, Forficulidae, Thysanoptera, etc., or with his Blattaeiformia, which includes such markedly differing forms as the Mantidae, Psocidae, Pediculidae, etc. Lameere, 1908, p. 141, says, " I am perfectly in accord with Handlirsch with regard to the composition of this systematic unity (the Neuropteroidea) formed of the Megaloptera, Raphidoidea and Neuroptera properly speaking (*i. e.* the Hemerobiiformia), and it is evidently the Megaloptera which exhibit the most archaic characters of the group," so that he evidently accepts Handlirsch's division of the order Neuroptera into these three orders. On page 297 of the Ent. News, vol. 27, 1916, I suggested that in addition to Handlirsch's subdivisions, the Neuroptera Planipennia might be further divided into a Mantispid group, a Myrmeleonid group, a Chrysopid group, and a Nemopterid group—the latter leading to the Mecoptera, with which they are united by Navas, 1905, in his book on the insects found in the neighbourhood of Madrid. If the Neuroptera were split into three distinct orders as Handlirsch has done, these groups might be regarded as suborders of the reduced order Neuroptera, with the exception of the Nemopteridae which are extremely closely related to the Chrysopid or Hemerobiid forms. Neither these subdivisions of the Planipennia nor Handlirsch's subdivisions of the Neuroptera are as distinct from one another as the Mecoptera are from the Neuroptera, however, and a rather extensive study of the thoracic sclerites of a number of types from Handlirsch's three orders of " Neuropteroidea " has revealed such a marked uniformity of structure in all three, that I have become convinced that these insects constitute but a single order, the Neuroptera. On the other hand, the sclerites of the Mecoptera and Trichoptera are sufficiently different from those of the Neuroptera to justify placing them in distinct orders, and since the thoracic sclerites have proven to be extremely

"conservative" structures varying but little within an order, I think that the evidence they offer is of the utmost importance for any phylogenetic study.

With regard to the origin of the Neuroptera, Handlirsch would derive them directly from the Palaeodictyoptera, while Lameere is inclined to derive the Neuroptera from Megasecoptera, and would also derive the other holometabolous insects such as the Hymenoptera and Coleoptera from the same source. The resemblance between the larvae of the Coleoptera and those of the Neuroptera is very marked (Proc. Ent. Soc. Washington, vol. 20, p. 58), and, superficially at least, such primitive Coleoptera as *Calopteron* appear quite like certain Neuroptera; but a study of the structural details of the Coleoptera would point to a closer relationship with the Dermaptera and other members of the Plecopteroid superorder, and such resemblances as occur between the Coleoptera on the one hand, and the Psocidae and Neuroptera on the other, might possibly be explained as the result of the retention in each of certain features inherited from a common Plecopteroid ancestry.

As was stated at the beginning of the paper, I am inclined to regard the Neuroptera as the descendants of ancestors more directly related to the members of the Plecopteroid superorder; but ultimately descended from forbears related to the Ephemerid group, which contains the Palaeodictyoptera. Tillyard, 1917 (Biology of Dragonflies, p. 8), is inclined to consider that the Neuroptera are somewhat closely connected with the Odonata by the "very ancient Protascalaphine genus *Stilbopteryx*." Haeckel, 1866 (Gen. Morphol.), derives the Neuroptera from "Pseudoneuroptera," and many of the older writers grouped the Neuroptera with the Odonata and Ephemerida. Thus Clairville, 1798 (Ent. Helvet.), according to Handlirsch, includes the Odonata, Ephemerida, Plecoptera, and the Neuroptera, together with the Mecoptera, Trichoptera, etc., under the designation Dictyoptera—a designation applied by Brullé, 1832, to the Odonata, Ephemerida, and Plecoptera, and by Leach, 1817 (Zool. Misc., 3), to the Blattidae and Mantidae. There are considerable grounds for considering that the Ephemerida are quite closely related to the Neuroptera and that the Odonata are also quite closely related to them; but the closest affinities of the Neuroptera are with the insects whose lines of descent are shown in Fig. 2.

Certain of the earlier entomologists (*e. g.* Latreille, 1831, Newman, 1834, etc.), and more recently Banks, are inclined to include the Isoptera with the Neuroptera. The Mantidae (which belong in the same superorder with the Isoptera) also show some affinities with the Neuroptera; but I am inclined to interpret these resemblances as the result of the retention of certain primitive features inherited from the common Plecopteroid ancestry from which were derived the Isoptera, Mantidae, etc., on the one hand, and the Neuroptera, with their allies, on the other. Through this Plecopteroid ancestry, the line of development of the Neuroptera leads back ultimately to forbears related to the Palaeodictyoptera, and other insects belonging to the Ephemerid group (in which the Megasecoptera might also be included). The relationship of the Neuroptera to the Mecoptera certainly seems very much closer than would be indicated by Handlirsch's deriving the Mecoptera from Megasecoptera while deriving the Neuroptera from Palaeodictyoptera; and the facts of comparative anatomy (not based upon the study of wings alone) would certainly appear to be more in harmony with the derivation shown in Fig. 2, in which the lines of descent of the Mecoptera and their allies are represented as quickly merging with that of the Neuroptera, which soon unites with the main stem of the Psocidae and their allies to form a main Neuropterous group stem. This in turn merges with the lines of development of the Plecopteroid forms, which are later joined by the lines of development of the Megasecoptera, Palaeodictyoptera and other insects belonging to the Ephemerid group.

It may be mentioned in closing, that the insects related to the Neuroptera fall into two superorders, each of which contains some insects very closely allied to certain members of the other superorder; but each group is fairly well defined. Of these insects, the Neuroptera, Lepidoptera, Trichoptera, Mecoptera, Diptera, Siphonaptera and the Hymenoptera (together with their fossil relatives) may be grouped in a superorder called the PANNEUROPTERA (Psyche, vol. 25, 1918, p. 55), characterised in general by the retention of five segments in the tarsi, the division of the mesothoracic coxae by an approximately vertical suture (which is present in the lower representatives of the Diptera, despite the frequent statements to the contrary—see Crampton and Hasey, 1915, "The Basal Segments of the

Leg in Insects," Zool. Jahrb., Abt. Anat., 39, pp. 1–26), the internal development of the wings, complete metamorphosis, etc.; while the Psocidae, Mallophaga, Pediculidae, Hemiptera and Homoptera, with their fossil relatives (and possibly including the Thysanoptera also) may be grouped in a second superorder called the PANHOMOPTERA (Psyche, *l.c.*), characterised in general by the reduction of the number of tarsal segments to not more than three, no division of the mesothoracic coxae (save in rare instances), external development of the wings, and practically no marked metamorphosis. There are some exceptions; but for the most part, these characters hold good for the more primitive representatives of each group.